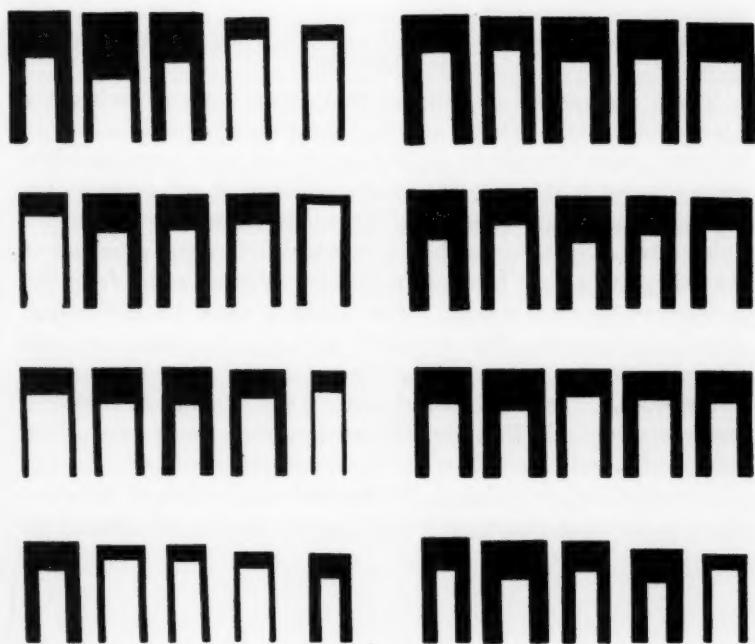


A

*Iris virginica*

B

*Iris versicolor*



C

West St. Ignace, Mich.

D

Engadine, Mich.

Fig. 20. Ideographs of twenty individuals each of the two hybrid colonies studied: C, West St. Ignace, Mich.; D, Engadine, Mich.; above, average colonies of *I. virginica* and *I. versicolor* for comparison.

eastern one, *Iris versicolor* L., and a southern and a middle-western one, *Iris virginica* L.

Statistical studies have been made of 16 colonies of *Iris versicolor* and 39 of *Iris virginica*. Each species is found to be a natural group. In spite of wide variation within each species there is no tendency whatsoever for one to merge into the other, and the general average of each species is practically the same wherever it is studied. Although variation between individuals is met with in every colony examined it has not resulted in any appreciable regional differentiation, since the species in question moved into their present home at the close of the glacial period.

*Iris versicolor* and *Iris virginica* are kept separate in part by natural geographical barriers and in part by physiological differences which prevent them from being perfectly fertile with each other. Along the narrow zone where the two species come in contact hybridization occasionally takes place. Natural hybrids, closely resembling those produced experimentally, have been found at five points. At two of these localities hybrid populations of considerable size had arisen and have been studied in greater detail. There is some evidence that constant new forms might originate in this manner.

## VI. DISCUSSION

There are several objections which must be met before the above conclusions can be accepted as generally applicable. In the first place it might be argued that there were regional differences present within the two species which were not revealed because of the methods used, the characters chosen for study, etc. It is quite possible that such unrecognized differences existed, but if so they must have been of an entirely different order from the differences between species. The methods used *did* distinguish effectively between *Iris versicolor* and *Iris virginica* and did demonstrate that no such differences existed within either of the two species. For the material studied the conclusion therefore seems unavoidable that *the differences within species are of an entirely different nature from the differences between them.*

A more valid objection to the general application of the conclusions drawn in this work is that the two species belonged to an

old and well-defined genus and that different relations between species might be found to obtain in such a group as the genus *Aster*, for instance. From purely *a priori* reasoning it would seem quite possible that distinctions between species might be of a different nature in different parts of the vegetable kingdom. Conclusions drawn from a study of two species belonging to the Monocotyledons would certainly have to be confirmed with more closely related material before they could be accepted as valid for such a distantly related group as a genus of the Compositae.

Another hindrance to the general application of the conclusions reached in the study of these two species is the geophysical nature of the region in which they occur. It is without great barriers of any sort. With a greater degree of isolation, such as would occur in a region cut by great mountain chains, the differences *within* species might perhaps be very different. It would be particularly interesting to compare the regional differentiation of the closely related western species, *Iris missouriensis*.

#### LINNAEAN VS. JORDANIAN SPECIES

The main conclusion drawn from this investigation is that the Linnaean species is a natural and permanent group. It should therefore be the most effective one for purposes of classification. In regard to Jordanian species I am in complete agreement with Clausen ('27) when he says, "The old botanists worked according to their own common sense and delicate biological feeling, but they had a conception of species far more nearly coinciding with what we now arrive at by careful statistical observation of variation in the field and by cytological investigations and crossing experiments than our modern small-species taxonomists. 'Eine Art ist eine Art, ganz gleichgültig ob sie *Diapensia lapponica*, *Viola tricolor*, oder *Hieracium marginelliceps* heisst', says du Rietz. I quite agree that it is a matter of supreme indifference to Nature what *we* decide shall be the definition of a species. But it is by no means a matter of indifference to ourselves whether we accept or reject a form of nomenclature which obscures Nature's own chief system of division."

In my opinion those who have considered the Jordanian to be of prime importance, taxonomically and phylogenetically, have

ascribed undue significance to the fact that it comes true from seed. With more genetical or horticultural experience they would have realized that coming true from seed (homozygosity) is a mere corollary of the amount of inbreeding which has taken place and that it is of minor taxonomic and phylogenetic significance.

We can best demonstrate the actual significance of the Jordanon's true-breeding quality by examining the relationships between individuals in two different sorts of species; in one continuously cross-pollinated and in one continuously self-pollinated. These relations are diagrammed in fig. 21 at a and b. Let us take four individuals of a continuously cross-pollinated species, such a one as *Aster anomalus*, for instance, to name one that has actually been investigated (unpublished data). We may diagram these four individuals as A, B, C, and D (b, fig. 21) and if we examine them they will be found to possess certain inherent differences in such characteristics as the number, length, and shape of the ray flowers, the number and arrangement of the branches of the inflorescence, etc. Though two individuals may sometimes agree in a single characteristic, no two will possess the same combination of characters. In the next generation, however, none of these particular combinations will reappear. Plant A will be pollinated by pollen from other plants, as, for instance, by B as in the diagram, and the resulting offspring will show new combinations of characters unlike anything in the previous generation. In the diagram one of them is taken as an example and named L. Plants M, N, and O are similar new combinations arising from cross-pollinations between the other plants of the previous generation. There will be similar new recombinations of characteristics for each new generation. In other words, there will be just such a reshuffling of characteristics as occurs from generation to generation in human families; man being another species in which similar out-crossing prevails.

If we now turn to a self-pollinated Linnaean species and study the differences between individuals we will find that they are very similar to those studied in *Aster anomalus*. We may therefore diagram them similarly (a, fig. 21) as A, B, C, and D. In such a self-pollinated species, however, a single individual acts as father and mother for the next generation. There will ordinarily

be no crosses between A and B or B and C as there were in *Aster anomalus*. Furthermore, since such close inbreeding has obtained in the past, each individual will be practically homozygous (pure-breeding), and its progeny will resemble their parent and each other very closely. The seedlings of A will be so similar to their parent that they can be diagrammed as A, those of B will show the same combination of characters which distinguished B from A, C, and D, and may be diagrammed as B. This resemblance will continue from generation to generation as long as no cross-pollination occurs. Such a species is therefore divisible into a number of pure lines or Jordanons.



Fig. 21. Diagrammatic representation of the relationships between individuals in a, a self-pollinated species, b, a cross-pollinated species, and c, in *I. versicolor*.

It will be seen that the reappearance of distinctive combinations of characters from generation to generation is a mere corollary of the amount of inbreeding. Those Linnaean species which are continuously cross-pollinated will form new combinations in every generation. Those which are continuously self-pollinated will be divisible into recognizable pure lines or Jordanons. If species were of only these two sorts it might be possible to retain the Jordanon as an auxiliary unit, useful in the one case but not in the other. Unfortunately there is every transitional stage between the two extremes. *Iris versicolor* and *Iris virginica* are species of this intermediate sort. As has been shown above, *Iris versicolor* is usually self-pollinated though occasionally out-crossed. The relationships between individuals may therefore be diagrammed somewhat as in c of fig. 21. The diagram may be taken as typical of many species which can be only partially

separated into Jordanons. Those individuals, such as plants A, B, C, and D in the diagram, which have resulted from a long line of self-pollinations will give rise to true-breeding strains as long as they are self-pollinated. But when a cross-pollination occurs, as when A is crossed with B, it produces new recombinations of characteristics. In the diagram one of these new individuals, L, is taken as an example. Even though self-pollinated it will not breed true and its offspring will vary among themselves. One of them is represented in the diagram and named T. Plant T will likewise be too heterozygous to breed perfectly true, and its progeny must be given a new symbol in the diagram. So even though continuous self-pollination occurs among the progeny of the cross between A and B, it will take six or more generations before pure breeding Jordanons will be established.

Borrowing an idea from the diagrams in fig. 21, we may think of each species as a net, with the knots representing individuals. Those species in which cross-pollination regularly obtains will have a very short mesh, interweaving from one generation to the next. Those species, such as *Iris versicolor*, in which it is rare, will have a much longer mesh with fewer connecting cross-threads. Some few species will be so seldom cross-pollinated as to seem hardly net-like in their make up. They will be more like separate and unconnected knotted strings, but it is to be doubted if even in such extreme cases there never occurs a cross-pollination which brings the strings of the net together. Even though they occurred on the average only once in forty or fifty generations, it would cause the ultimate interweaving of the whole net and the disappearance of the single strings as separate units.

The case for the Jordanon as a universally applicable unit becomes even more absurd when we consider the case of a species which is cross-pollinated in one part of its range and self-pollinated in another. While this has not been demonstrated for any wild species, there is no *a priori* reason why such a delicately balanced relation might not vary under different environments. Leighty and Taylor ('27) have called attention to the fact that this has actually occurred in wheat which has different percentages of natural outcrossing in different parts of the world, as, for instance, in the Punjab where Howard and Howard ('09) report a very high



percentage. It has been found for numerous species that they are cross-pollinated only by a single insect. Such a Linnaean species, cross-pollinated in one part of its range and self-pollinated in another, would be divisible into Jordanons in the latter region but not in the former.

The division of a Linnaean species into Jordanons is therefore seen to be a mere corollary of the amount of inbreeding which has obtained in that species. Where Jordanons do occur they owe their existence to continuous self-pollination and their individuality disappears as soon as a cross-pollination takes place. In those species where cross-pollination is of rare occurrence they will undoubtedly persist for some time, perhaps even for centuries, but they will ultimately disappear.

These studies have shown that the Linnaean species, on the other hand, may retain its individuality, though submitted to widely differing environments, for long periods of time. *Iris versicolor* and *Iris virginica*, for instance, must have persisted as recognizable units since they spread into their present homes at the close of the glacial period. Important as the Jordanon may be in the case of cultivated plants, or in those Linnaean species in which it naturally occurs, it is a relatively temporary unit of little taxonomic or phylogenetic significance.

There remains to consider the bearing of the studies reported above on the question of the origin of species. For the material studied it has been shown that *the differences between species are of an entirely different order from the differences between individuals*. There is no evidence that these differences between individuals might, under the influence of natural selection or of any other natural force, eventually be compounded into differences comparable to those between the two species studied. This conclusion is not in accord with most current speculation on the subject. Since the time of Darwin it has been very commonly supposed that the processes which give rise to differences between individuals, if allowed to operate over a longer period, will produce specific differentiation. This general theory has gone through many phases as biology has advanced; in its most recent form it is held by many of the *Drosophila* workers who see in the gene mutation the unit process which, compounded a thousand-fold, results in specific differences.

There is little in the evidence reported in this paper to support such an explanation of the origin of species. If all the individual differences which have occurred in *Iris virginica* since the glacial period have not produced recognizable regional differences within the species, the production of new species by this means must be a very slow process.

If we are to deny the slow accumulation of individual differences an important role in species building, to what process are we to turn? A number of recent investigators, Brieger ('28) Clausen ('27), Karpechenko ('27), to name only a few, have reported the experimental production of true-breeding hybrids as the result of new chromosomal realignments. The careful experimental investigation of these hybrids has strengthened the case of those who believe with Lotsy ('16) that hybridization has been an important factor in the evolution of species. Though it has not been investigated cytologically, the colony studied at Engadine is apparently composed of similar true-breeding hybrids of natural origin. While it will have to be very thoroughly investigated before it can be taken as conclusive, this apparent example of a new and constant form produced by the hybridization of two separate species is certainly very suggestive.

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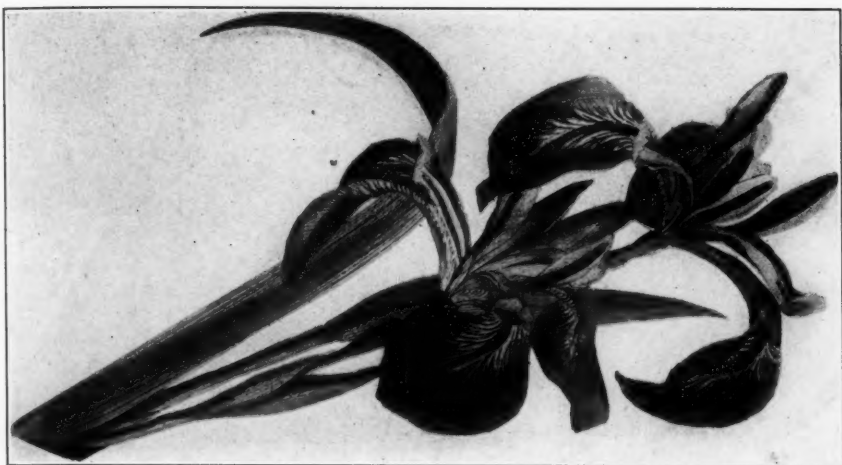
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## EXPLANATION OF PLATE

## PLATE 35

Fig. 1. *Iris latifolia Virginiana*, etc. Miller. From Ehret, G. D., *Plantae Depictae*, Tab. VI. 1748.

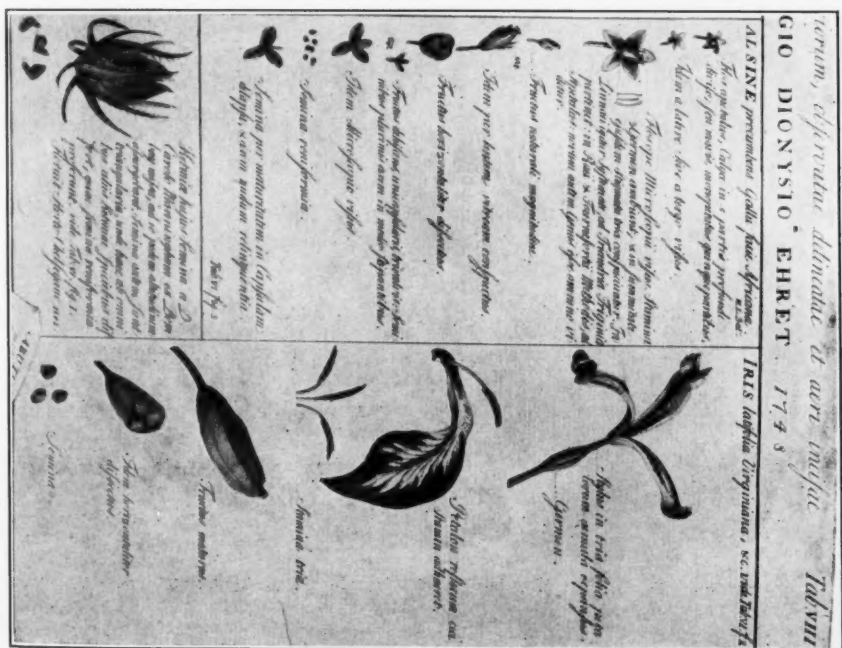
Fig. 2. *Iris latifolia Virginiana* etc. Miller. From Ehret, G. D., *Plantae Depictae*, Tab. VIII. 1748.



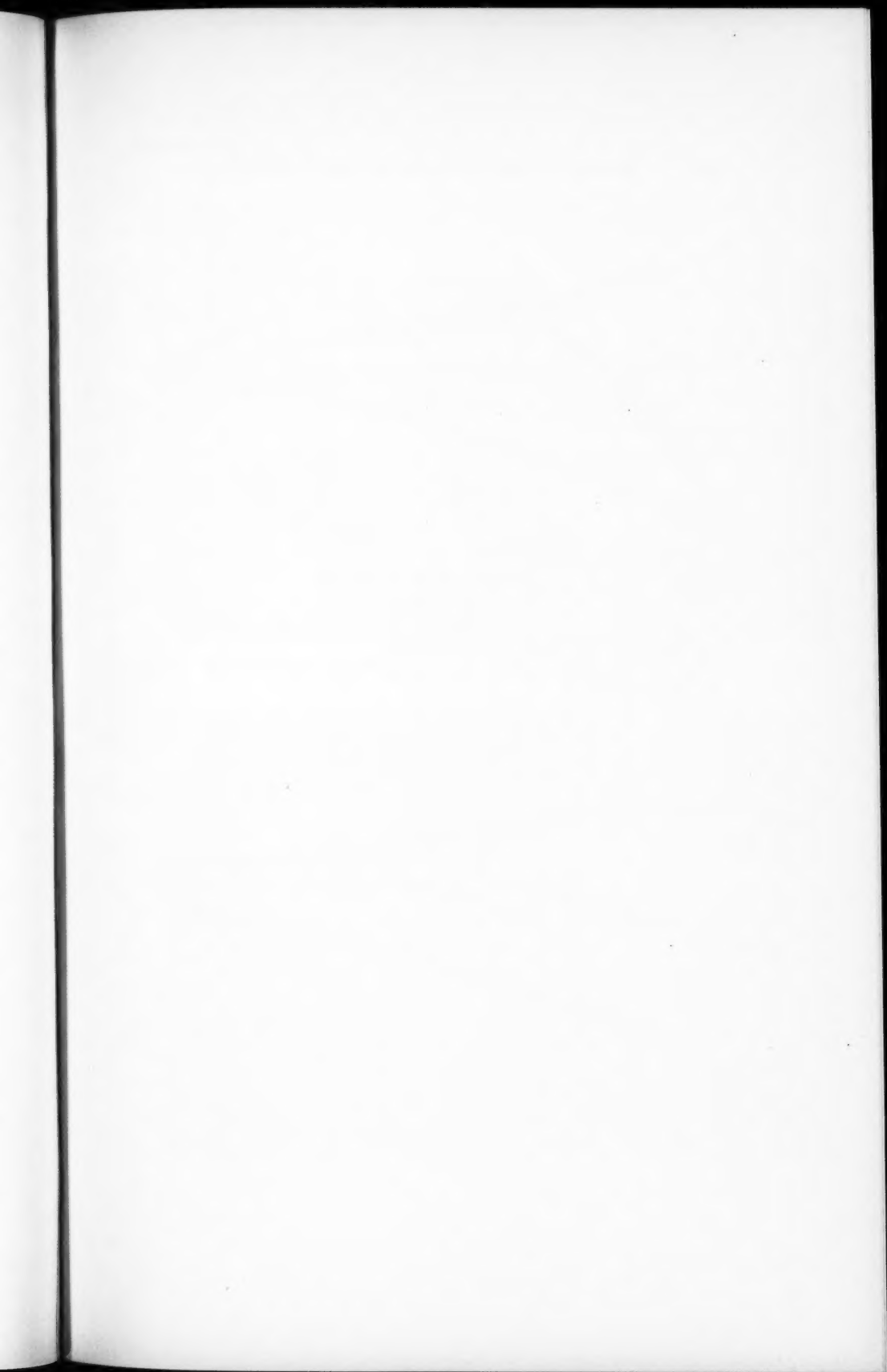
1

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2







## EXPLANATION OF PLATE

## PLATE 36

Fig. 1. *Iris versicolor* L. Dillenius' specimen of *Iris americana versicolor*, etc. deposited in the Dillenian Herbarium at Oxford.

Fig. 2. *Iris carolina* Radius. From Radius, W. M., Naturforsch. Ges. Leipzig Schrift. 1: 158. taf. III.







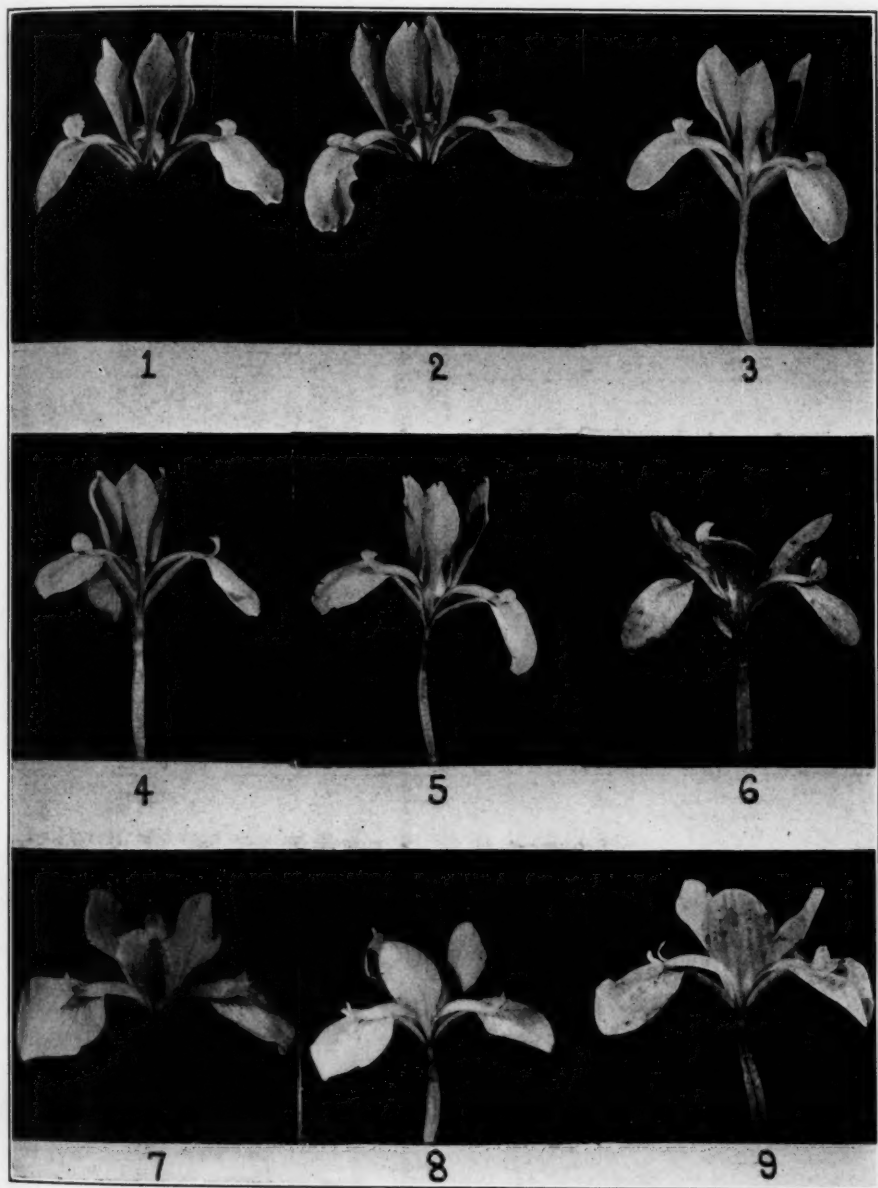


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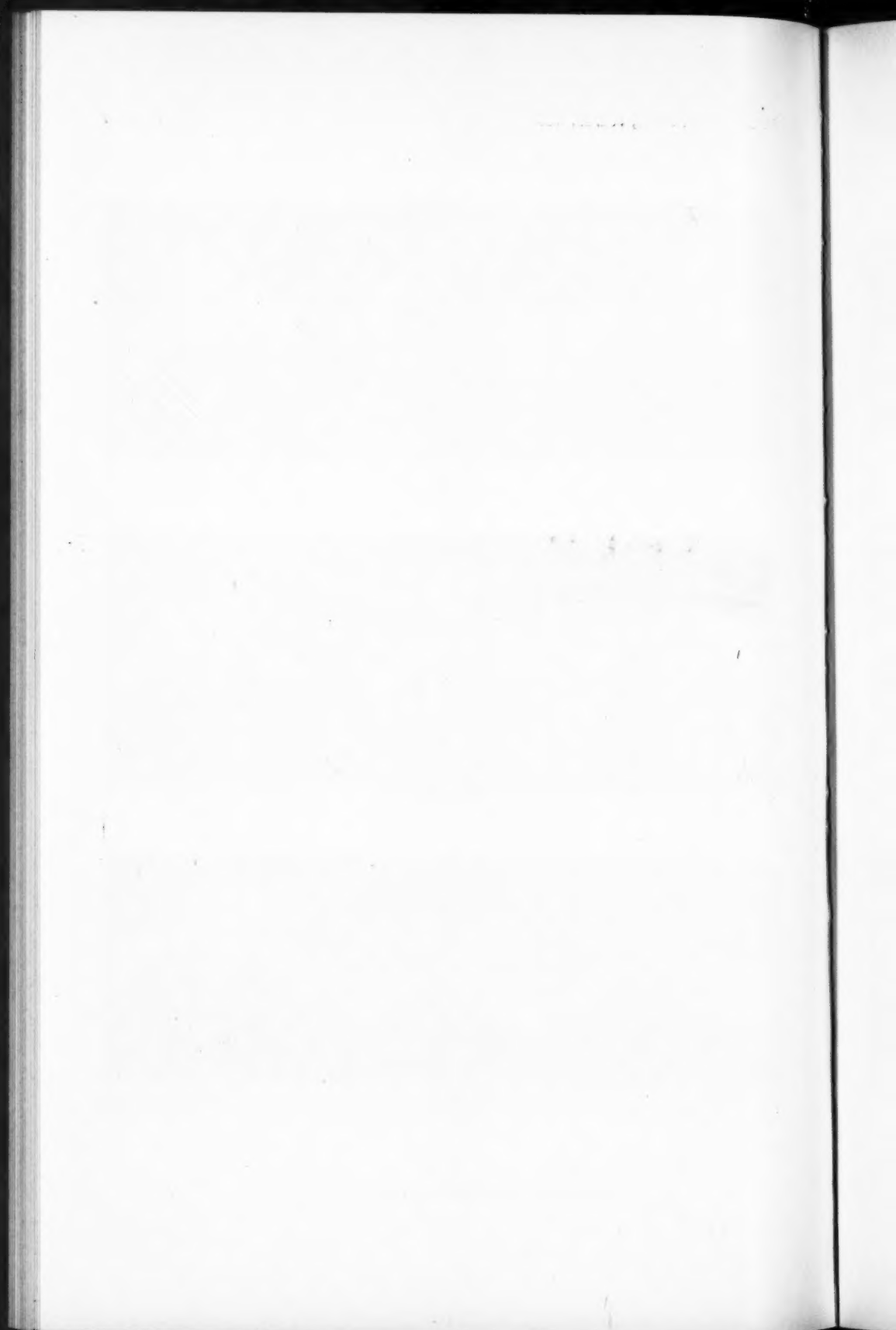
## PLATE 37

*Flowers of Iris virginica*,  $\times \frac{1}{2}$ 

- Fig. 1. Plant ABC—collected at Orchard Farm, Mo.
- Fig. 2. Plant ABC—collected at Orchard Farm, Mo.
- Fig. 3. Plant ABC—collected at Orchard Farm, Mo.
- Fig. 4. Plant ABC—collected at Orchard Farm, Mo.
- Fig. 5. Plant ABC—collected at Orchard Farm, Mo.
- Fig. 6. Plant ABE—collected at Fort Madison, Ia.
- Fig. 7. Plant ABE—collected at Fort Madison, Ia.
- Fig. 8. Plant ABE—collected at Fort Madison, Ia.
- Fig. 9. Plant ABQ—collected at Gilbertville, Ia.



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## EXPLANATION OF PLATE

## PLATE 38

Flowers of *Iris versicolor*,  $\times \frac{1}{3}$

- Fig. 1. Plant ABY—collected at Cohasset, Mass.
- Fig. 2. Plant ACF—collected at New Haven, Conn.
- Fig. 3. Plant ACF—collected at New Haven, Conn.
- Fig. 4. Plant BBG—collected at Harmonsburg, Pa.
- Fig. 5. Plant collected at Cedar Lake, Nova Scotia.
- Fig. 6. Partial albino, var. "Stella Main"—collected in Connecticut.
- Figs. 7-9. Seedlings grown at the Missouri Botanical Garden from seed collected at Connecticut Lakes, N. H.



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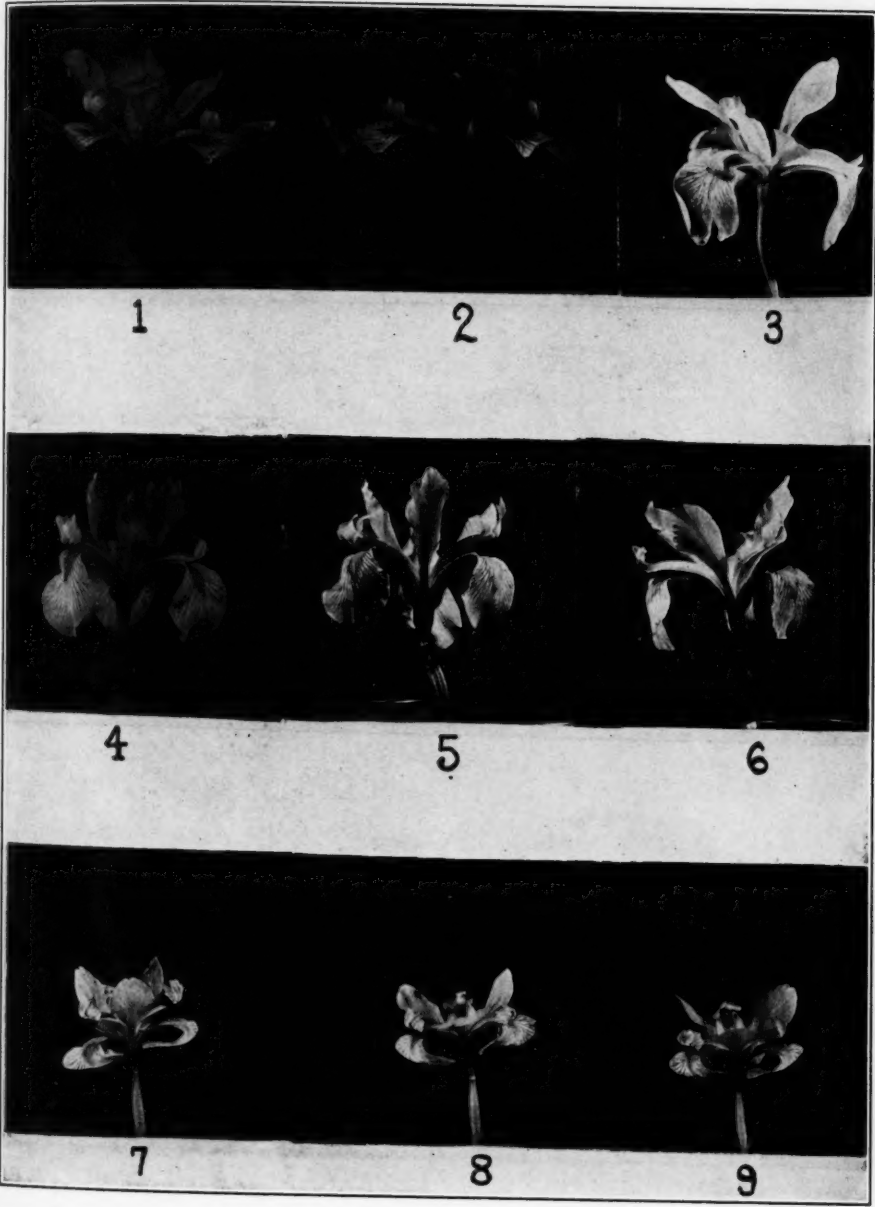
## EXPLANATION OF PLATE

## PLATE 39

Flowers of *Iris virginica*,  $\times \frac{1}{4}$ .

- Figs. 1-2. Plant ABB—collected at Valley Park, Mo.
- Fig. 3. Plant ACZ—collected at Fish Creek, Wis.
- Fig. 4. Plant ABT—collected at Yale, Mich.
- Fig. 5. Plant ABT—collected at Yale, Mich.
- Fig. 6. Plant ABT—collected at Yale, Mich.
- Fig. 7. Plant ABP—collected at Otisville, Mich.
- Fig. 8. Plant ABP—collected at Otisville, Mich.
- Fig. 9. Plant ABP—collected at Otisville, Mich.





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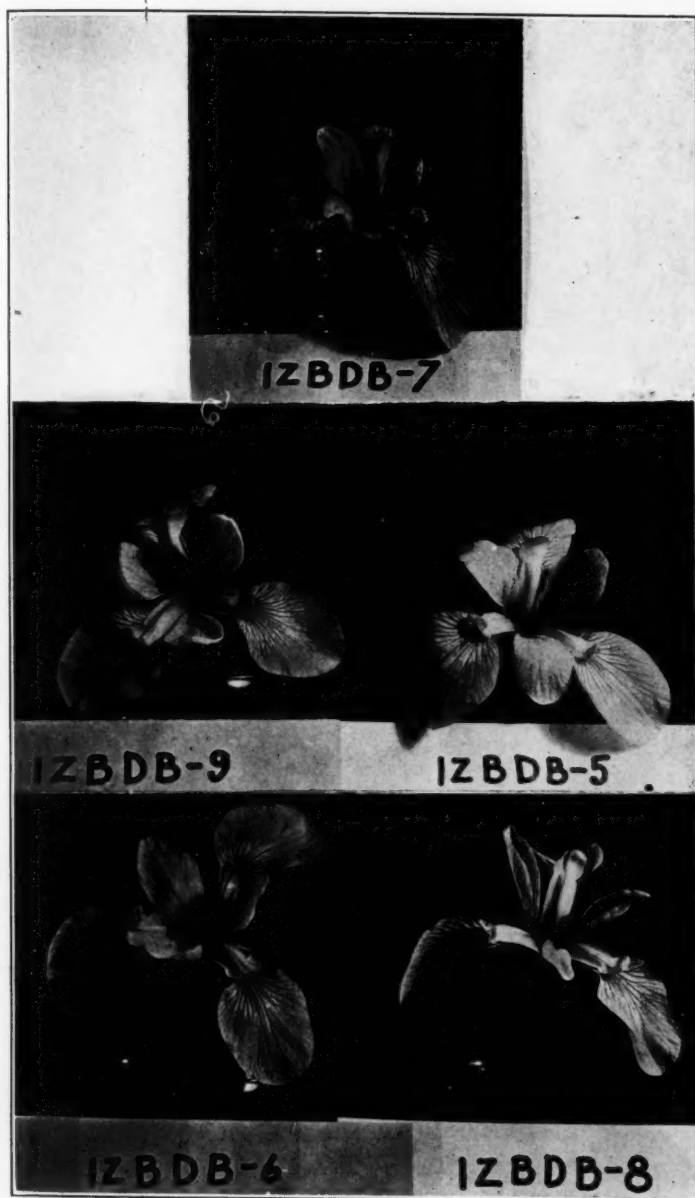




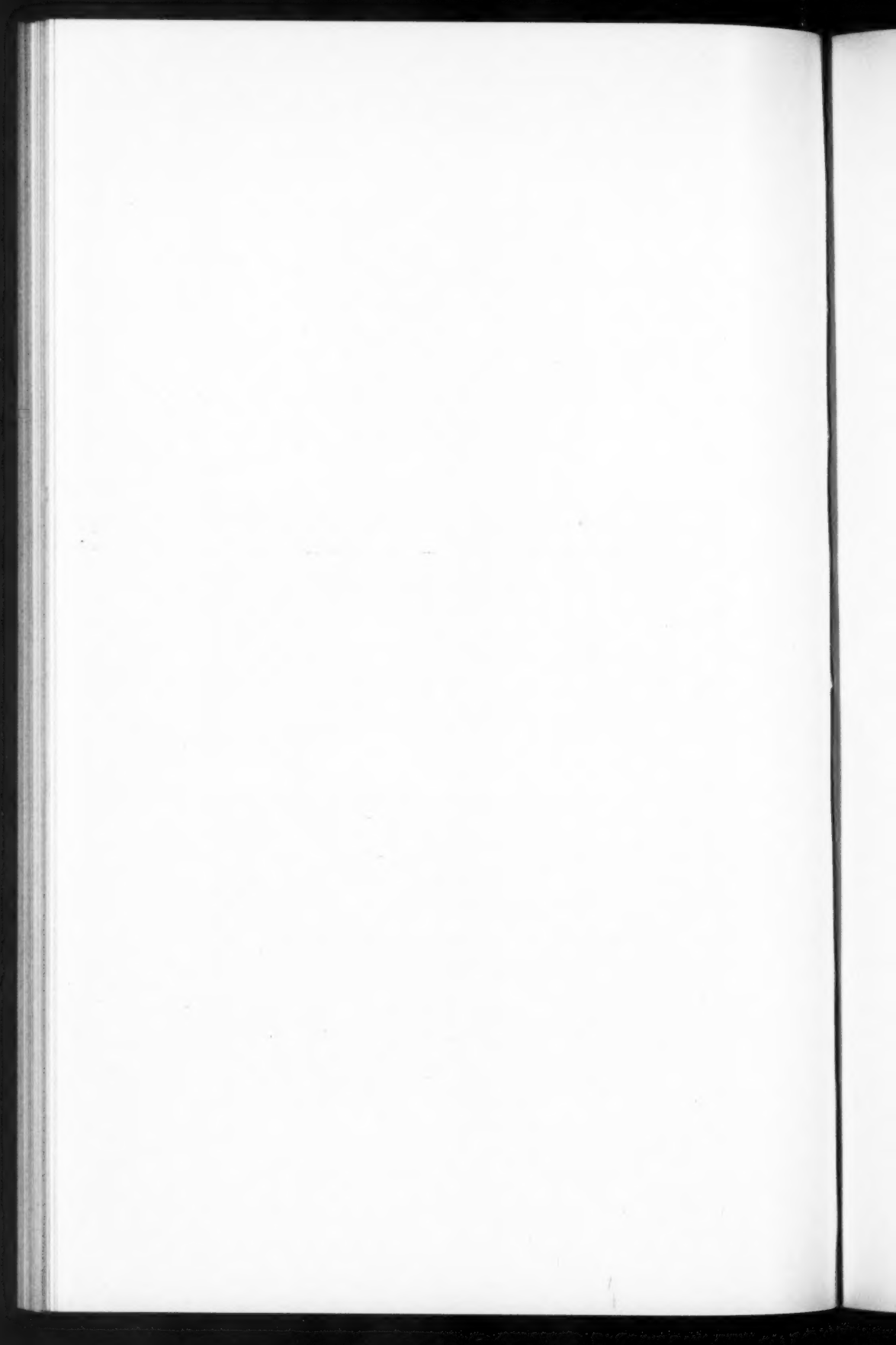
## EXPLANATION OF PLATE

## PLATE 40

One flower each of five sister plants of *Iris versicolor* grown at the Missouri Botanical Garden from a seed capsule collected at Connecticut Lakes, N. H.



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## EXPLANATION OF PLATE

## PLATE 41

A comparison of *Iris versicolor* and *Iris virginica* with *Iris*  $\times$  *robusta*, the hybrid between them.

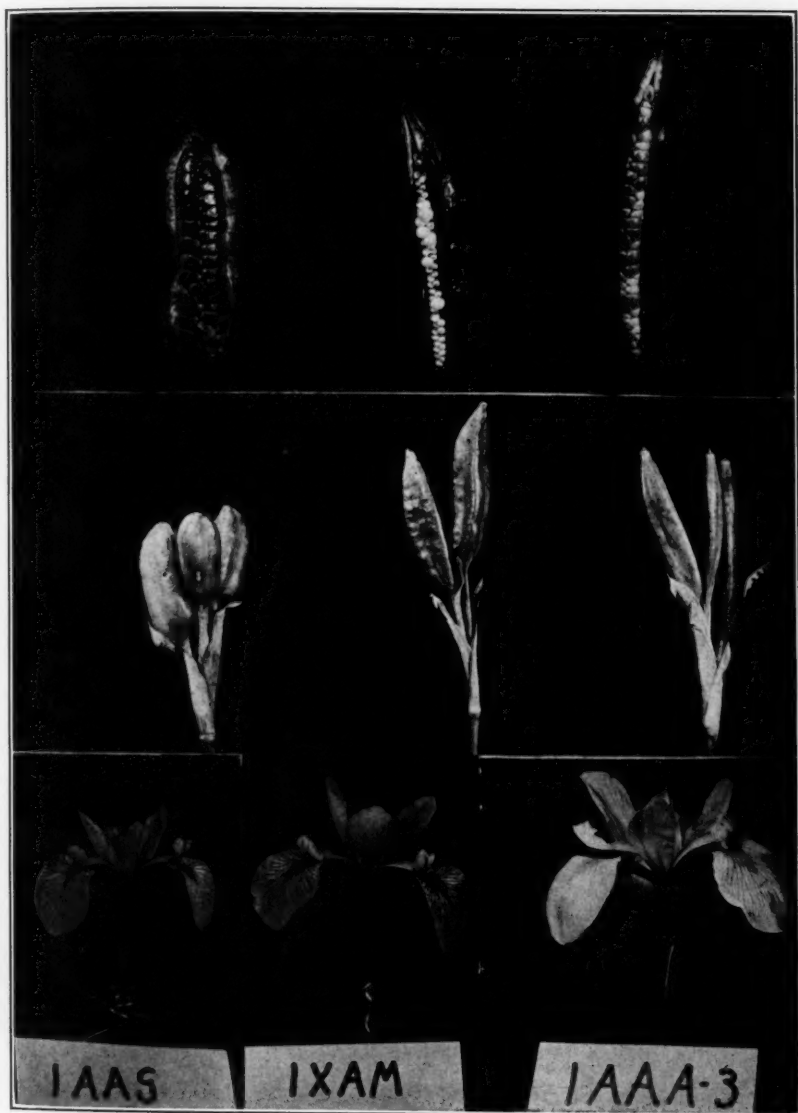
Top row, immature capsules with one locule exposed.

Middle row, immature capsules.

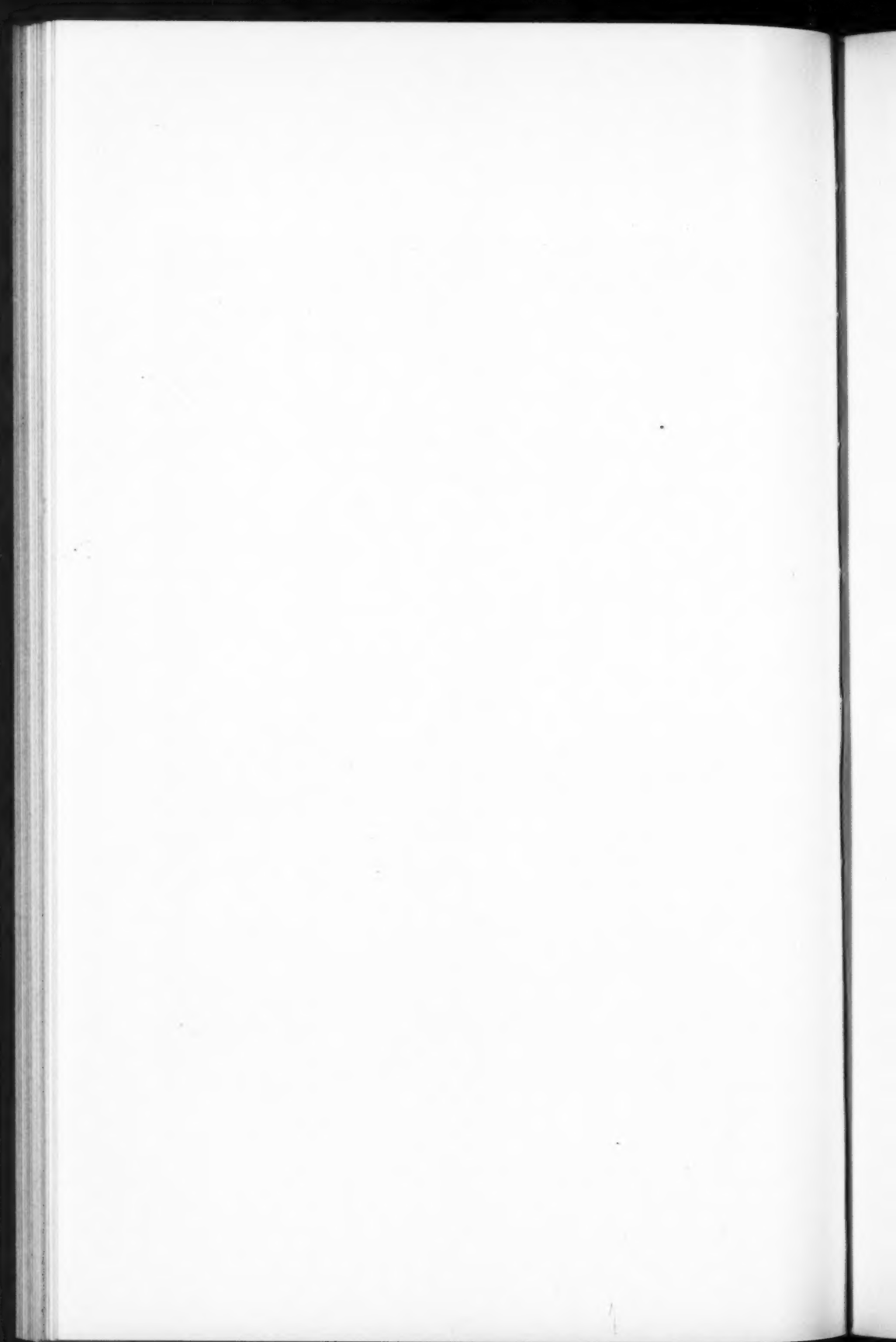
Bottom row, flowers.

In each case the specimen at the left is from plant IAAG (*Iris versicolor*), that at the right from IAAA-3 (*Iris virginica*), and that in the center from their hybrid IXAM (*Iris*  $\times$  *robusta*).





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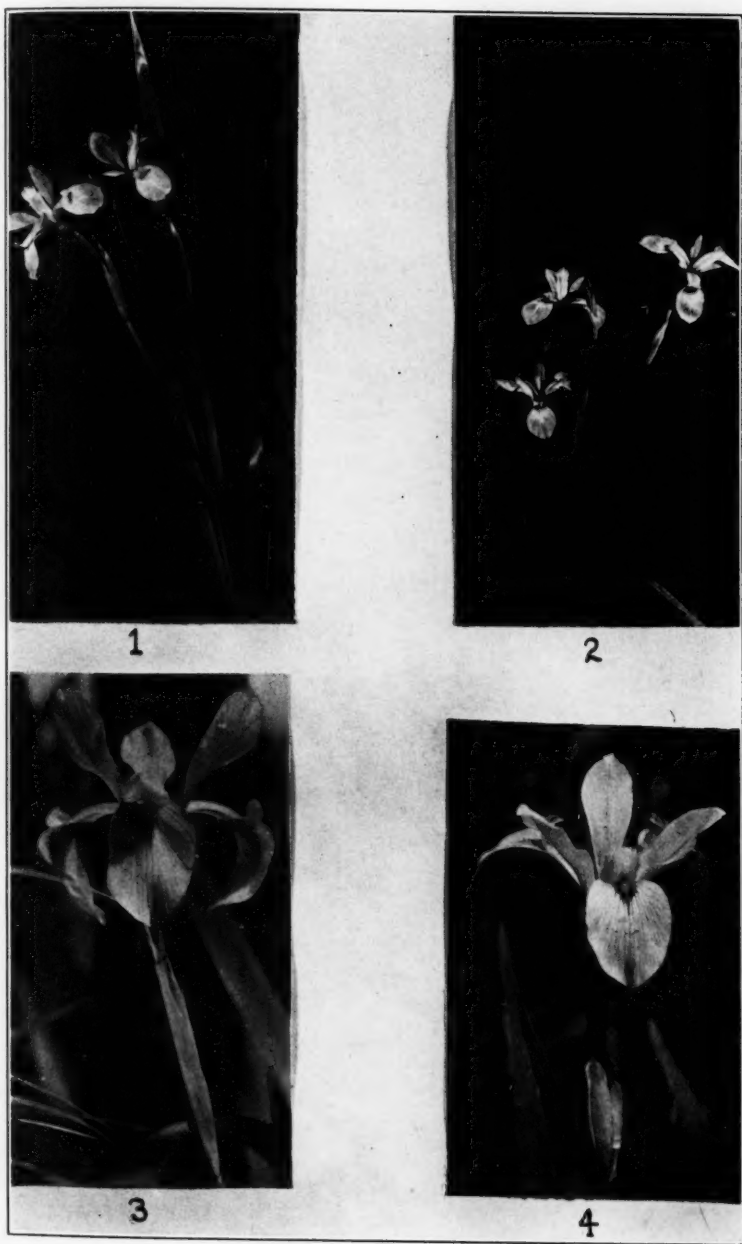




## EXPLANATION OF PLATE

## PLATE 42

- Fig. 1. Typical flower stalk of *Iris virginica*.
- Fig. 2. Typical flower stalk of *Iris versicolor*.
- Fig. 3. *Iris virginica* photographed at Huntingdon, Tenn.
- Fig. 4. *Iris virginica* photographed at Wilmington, N. C.



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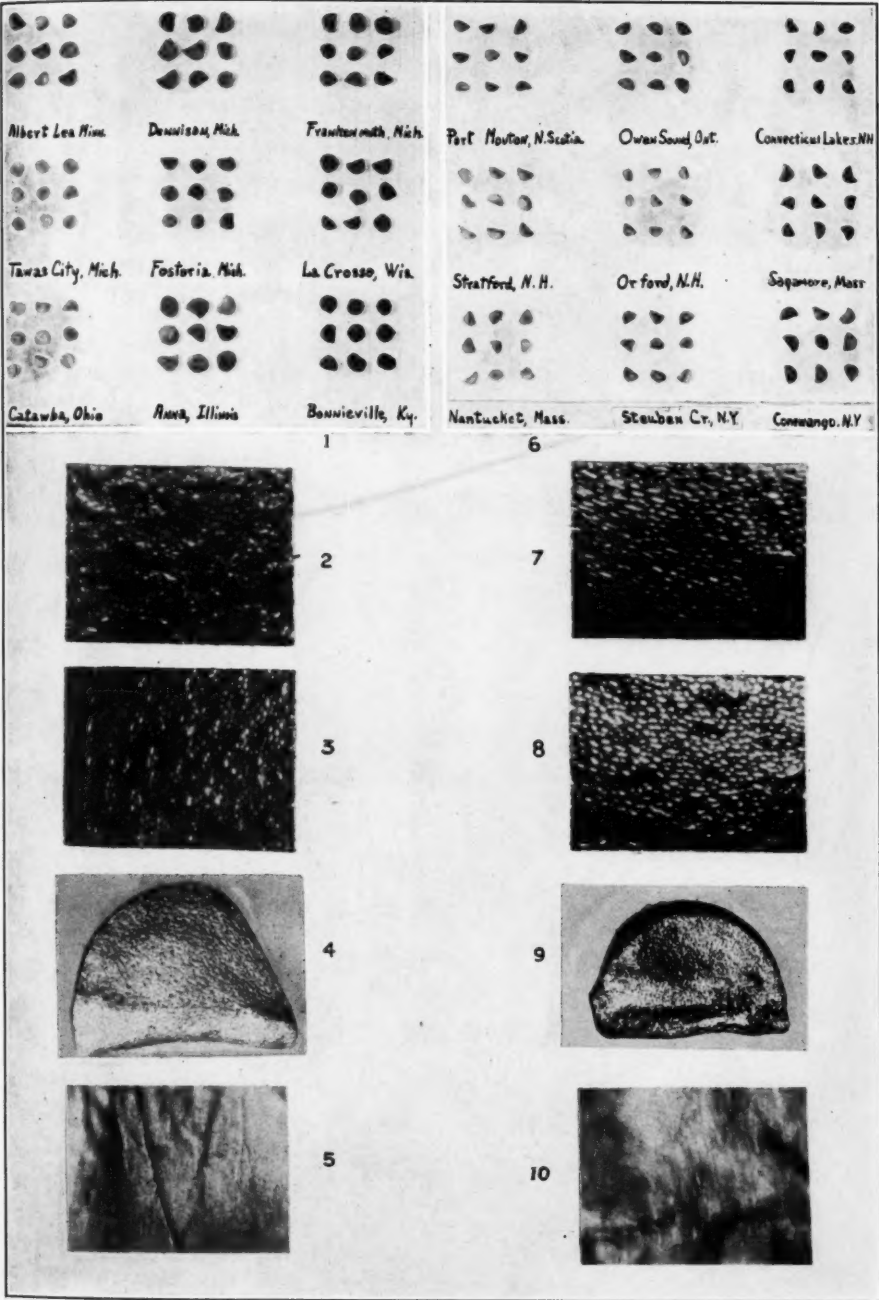


## EXPLANATION OF PLATE

## PLATE 43

Figs. 1-5. *Iris virginica*.Fig. 1. Collected seeds from nine localities,  $\times \frac{1}{2}$ .Fig. 2. Seed surface (St. Louis, Mo.),  $\times 30$ .Fig. 3. Seed surface (Catawba, Ohio),  $\times 30$ .Fig. 4. Seed,  $\times 7$ .Fig. 5. Lining of seed capsule,  $\times 30$ .Figs. 6-10. *Iris versicolor*.Fig. 6. Collected seeds from nine localities,  $\times \frac{1}{2}$ .Fig. 7. Seed surface (Sagamore, Mass.),  $\times 30$ .Fig. 8. Seed surface (Conewango, N. Y.),  $\times 30$ .Fig. 9. Seed,  $\times 7$ .Fig. 10. Lining of seed capsule,  $\times 30$ .





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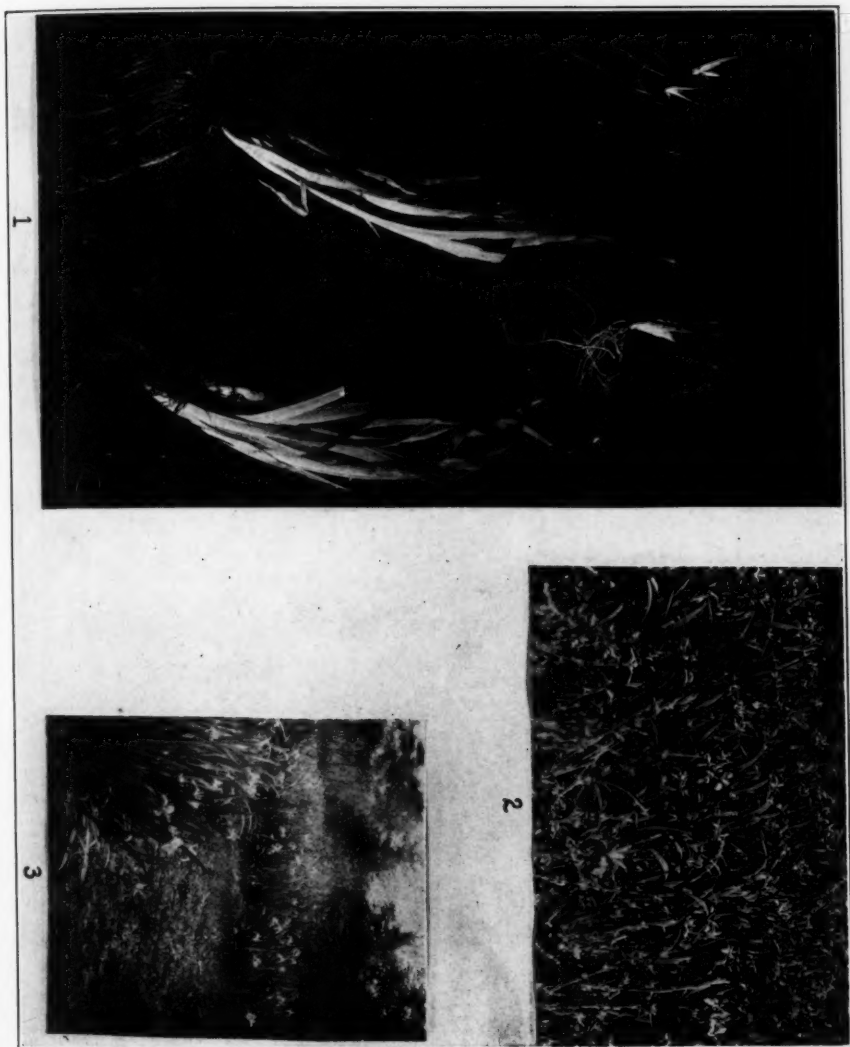
## EXPLANATION OF PLATE

## PLATE 44

Fig. 1. Upper row, two plants of *Iris virginica* from Valley Park, Mo., grown in cinders along railroad track; lower row, two plants from the same colony but growing in rich swamp.

Fig. 2. Large single clone of *Iris virginica*, Maysville, N. C.

Fig. 3. Colony of *Iris virginica* at Camden, Tenn.



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2000

1000

1000